

FOOD STORING IN THE PARIDAE

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ABSTRACT.—Food storing is widespread in the Paridae. Chickadees and tits store seeds, nuts, and invertebrate prey in a scattered distribution within their home range. They can establish hundreds to thousands of caches per day, and place only one, or a very few, food items at each cache site. Field experiments show that food is collected a few days after caching it, but there are also indications that stored food may remain available for longer periods. Behavioral and neurophysiological studies show that memory for the spatial locations of cache sites is the primary method used to retrieve stored food. The hippocampus plays an important role in the kinds of memory used to recover stored food, and is larger in size in families such as the Paridae in which food storing is common. The ecological and evolutionary relations between food storing and diet, body size, seasonality of the food supply, memory, and social organization are not well understood, but study of the Paridae can help to answer many of these questions.

The Paridae is one of several families of birds in which food storing is common. Food storing also occurs in many woodpeckers, nuthatches, and corvids, in a variety of raptors, shrikes, and bellmagpies (Cracticidae), in some muscicapid flycatchers (Powlesland 1980), and in bowerbirds (Pruett-Jones and Pruett-Jones 1985). Fourteen species of chickadees and tits are known to store food, and the behavior is known not to occur, or to occur very rarely, in two others (Table 1). That leaves thirty-one species for which there is no information on the occurrence of food storing. The behavior of many of these parids is not well known, and food storing may have been overlooked or not reported in others. This paper describes food storing as it occurs in chickadees and tits, emphasizing research on the role of memory in the recovery of caches of stored food.

One of the earliest descriptions of food storing by any bird is that of Johann Ferdinand Adam Pernau, Baron von Perney (1660-1731). His observations and methods were very sophisticated for their time but were practically unknown until their rediscovery by Stresemann (1947). In a book engagingly titled "Agreeable Country Pleasures (Angenehme Landlust)," Pernau writes: "He that searches for a proof of animals having some kind of reason, may allow a Marsh Tit ('Hanfmeise,' *Parus palustris*) to fly about in his room in which a tree was set where she can live. After she gets used to that room, one has to withhold food from her for half a day and then to strew uncrushed hemp on the table, or on the floor. Immediately the Marsh Tit will come and carry away in her bill three or

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TABLE 1
FOOD-STORING PARIDS

Common Name	Species	Status*	Source
Marsh Tit	<i>Parus palustris</i>	S	Löhrl 1950
Sombre Tit	<i>Parus lugubris</i>	S	Löhrl 1966
Willow Tit	<i>Parus montanus</i>	S	Haftorn 1956b
Black-capped Chickadee	<i>Parus atricapillus</i>	S	Butts 1931
Carolina Chickadee	<i>Parus carolinensis</i>	S	Brewer 1963
Mountain Chickadee	<i>Parus gambeli</i>	S	Haftorn 1974
Siberian Tit	<i>Parus cinctus</i>	S	Haftorn 1973
Boreal Chickadee	<i>Parus hudsonicus</i>	S	Haftorn 1974
Chestnut-backed Chickadee	<i>Parus rufescens</i>	S	Varley 1974
Coal Tit	<i>Parus ater</i>	S	Haftorn 1956a
Crested Tit	<i>Parus cristatus</i>	S	Haftorn 1954
Great Tit	<i>Parus major</i>	NS	Haftorn 1956c
Blue Tit	<i>Parus caeruleus</i>	NS	Haftorn 1956c
		S	Richards 1958
		S	Southern 1946
		S	Hinde 1952
Varied Tit	<i>Parus varius</i>	S	Higuchi 1977
Plain Titmouse	<i>Parus inornatus</i>	S	Davis Davis and Davis 1973
Tufted Titmouse	<i>Parus bicolor</i>	S	Bent 1946

* S = storing; NS = nonstoring.

four grains all at once. . . she will place all the others on a thick branch next to the stem, and then proceed to eat the first grain, frequently at quite another spot in the room. This done, she will fetch the rest of the hidden grains, one by one . . ." (translation by Stresemann 1947, p. 48).

Pernau provides a remarkably accurate description of the basic methods that are used today for observing food storing by chickadees and tits in captivity. Other early descriptions of food storing by parids can be found in Bechstein (1840) and Fatio and Studer (1889), along with a series of anecdotal observations in the journal *British Birds* (e.g., Astley 1923, Lewis 1923, Hibbert-Ware 1929). Research on food storing entered the modern era with an impressive series of studies of several European parids by Svein Haftorn (Haftorn 1944, 1953, 1954, 1956a, b, c). In addition to work on the Paridae, food storing has been extensively examined in the nutcrackers, *Nucifraga caryocatactes* and *N. columbiana* (Swanberg 1951, Balda 1980, Tomback 1980, Vander Wall 1982, Kamil and Balda 1985), and a variety of other birds and mammals (Smith and Reichman 1984, Sherry 1985).

THE NATURAL HISTORY OF FOOD STORING IN THE PARIDAE

Chickadees and tits store seeds, nuts, insects, and other invertebrate prey in a scattered distribution within their territory or home range. They may store hundreds to thousands of food items per day (Haftorn 1954, 1959, Sherry et al. 1982, Pravosudov 1985), placing only one or a very few items at each cache site. Pravosudov (1985) estimated that the Siberian Tit (*P. cinctus*) and Willow Tit (*P. montanus*) in the Murmansk area cache about twice as much food as they consume on the spot, about 15 kg of pine seeds and invertebrates per bird annually. Haftorn (1959) estimated that a typical food-storing tit in the Trondheim area stores between 50,000 and 80,000 spruce seeds each autumn.

Typical cache sites include tree bark, moss, lichen, conifer needles, hollow stems, and buds. Cache sites may be at any height above the ground from a few centimeters to many meters, and Marsh Tits sometimes push food into the ground to store it (Löhr 1950, Gibb 1954, Cowie et al. 1981). Some species cover the cache with a piece of bark or lichen (Crested Tit [*P. cristatus*], Haftorn 1954, Varied Tit [*P. varius*], Higuchi 1977), and Haftorn (1974) reports Boreal Chickadees (*P. hudsonicus*) securing stored food in place with web and seed down. Most parids prepare insect material for storage by removing the head and sometimes other parts. The Crested Tit places such prepared insects at cache sites so that tissue fluids act as an adhesive with the substrate (Haftorn 1954). Cache sites are not re-used in the wild (Cowie et al. 1981, Sherry et al. 1982, Pravosudov 1985), and thus the number of different cache sites created roughly equals the number of items stored.

Food may be stored a few meters from where it was encountered (Pravosudov 1985) or carried distances of up to 100 meters (Richards 1958, Cowie et al. 1981, Moreno et al. 1981). The latter studies, reporting long carrying distances, were conducted at feeders with a fairly rich supply of storable food, while the former, reporting short carrying distances, describes encounters with natural food distributions. This difference in how far food is carried before storage may be due to how much storable food is available, how much has already been stored in the vicinity, or it may be a consequence of the presence of other birds at rich food sources (Sherry et al. 1982). Birds storing food are often pursued, usually by other parids or nuthatches which attempt to take the food or pilfer the cache after the food-storing individual has left (Löhr 1950, Richards 1958, Sherry et al. 1982).

Even after food has been successfully stored, the level of cache pilfering may be quite high. A rate of loss of 20% or more per day was found for Marsh Tit caches (Sherry et al. 1982). Some of this food was taken by

other birds, but the greatest source of loss was overnight pilfering by rodents.

Most available information indicates that food is recovered a few days after storing it, but these results do not rule out the possibility of long-term storage. In a study in which Marsh Tit cache sites were located by giving the birds sunflower seeds labelled with a low dose of radioactive technetium (Tc 99 m), it was found that stored seeds were taken within a few days after storing (Cowie et al. 1981). (Evidence that these seeds were recovered by the bird that stored them is described below.) Löhrl (1950) also reports that Marsh Tits collect their caches after several days. Stevens and Krebs (1986) equipped Marsh Tits with small magnets on their leg bands and placed detectors at cache sites to register visits by the birds. They confirmed that the bird that stores food returns to collect it, and that the interval between storage and recovery is rarely more than one or two days. Moreover, recovery attempts at the longest intervals were uniformly unsuccessful, because the caches had been pilfered in the meantime by other birds or rodents.

These results may not be the whole story, however. In captivity, Marsh Tits and Black-capped Chickadees (*P. atricapillus*) often retrieve food from one cache only to store it again elsewhere. This has also been reported in the wild (Haftorn 1954). It is therefore possible that food is taken from initial storage sites quite promptly but transferred to other long-term cache sites. Ludescher (1980) likewise suggests that there may be two modes of food caching in parids: long-term for winter food reserves and short-term to take advantage of encounters with rich food sources. There is presently no direct evidence that parids ever recover stored food after periods longer than a few days, largely because of the difficulty researchers have in tracking stored food for long periods. But there are indications of much longer term storage. Higuchi (1977) reports that 5% of the nestling diet of Varied Tits in May is made up of nuts of *Castanopsis cuspidata* which the adults store from August to February. Gibb (1960) reports Coal Tits (*P. ater*) eating caterpillars and pine seeds in winter, several months after these foods would be expected to be available. Haftorn (1956b) discovered *Galeopsis* seeds in the stomachs of Willow Tits in mid-winter, even though snow cover had prevented access to *Galeopsis* plants since the previous autumn. It is thus likely, though not conclusive, that in each case scarce foods were being taken from caches established several months earlier.

HOW IS STORED FOOD RECOVERED?

There are potentially many means by which caches of food could be relocated and exploited. Caches could be encountered at random during normal foraging like any other encounter with prey. By putting caches in

the kind of places where it normally forages, a chickadee or tit might eventually re-encounter most of its stored food. The major difficulty with this method is that other animals foraging in the same places would have an equal likelihood of finding the caches. A refinement on this method would be to store food only in particular locations, determined by some kind of "rule." The bird would have to search exhaustively at all sites satisfying the rule, but this would nonetheless confer an advantage over competitors searching for caches. The rule might differ among individuals, or it could vary within individuals from one bout of caching to the next. Alternatively, birds could mark caches in a distinctive way and search for these marks. If the marks were detectable from a distance, the bird could orient to them and quickly approach the cache. Finally, birds could remember the spatial locations of caches and return to them directly. Löhrl (1950) was the first to suggest seriously that chickadees and tits remember where they have cached food. In fact, he distinguished two kinds of memory that might be involved in relocating cache sites, the ability to recall spatial locations from memory (*freie Erinnerung*) and the ability to recognize a particular spatial location when it is encountered (*gebundene Erinnerung*). Much of the recent research on food storing by parids has examined these various means of cache recovery.

FIELD STUDIES

At cache sites found by searching for labelled seeds, as described above, Cowie et al. (1981) set up a simple field experiment. We placed two control seeds near the cache, at distances of 10 cm and 100 cm respectively, in sites that were as nearly identical as possible to the cache site chosen by the bird. Inspections of these trios of hidden seeds at intervals of three hours allowed us to monitor their disappearance. The logic of the experiment was that if Marsh Tits re-encountered their caches at random, then seeds in all three sites should disappear at the same rate. Any other animal taking seeds would also be expected to take cached and control seeds with equal frequency. We found that seeds stored by the birds were removed after a mean of 7.7 daylight hours, while the 10 cm and 100 cm control seeds remained in place for 13.5 and 20.4 daylight hours, respectively. On 93 out of 121 occasions, the cached seed was taken while the control seed 10 cm away was not. We interpret this result as showing that Marsh Tits do not re-encounter their caches at random, but that instead they return quite precisely to the place where food was stored.

These results, however, do not show unequivocally that memory is the means by which Marsh Tits return accurately to their cache sites. A number of laboratory studies of Marsh Tits and Black-capped Chickadees have addressed the question (Sherry et al. 1981; Sherry 1982; Shettleworth

and Krebs 1982, 1986; Sherry 1984a, 1984b; Sherry and Vaccarino, 1989; Baker et al. 1988). The basic design of these studies has been to compare the birds' observed accuracy in retrieving stored food to the accuracy expected by chance encounter or other methods of cache recovery.

LABORATORY STUDIES

Both Marsh Tits and Black-capped Chickadees adjust well to captivity. In the laboratory, it is much easier to control the conditions under which the birds search for the caches they have made. In most of these experiments the birds cache seeds in suitable sites that are provided, such as beds of moss or small holes in tree branches, and after a delay of several hours to several days, search for their caches. Usually the stored food is removed in the interval by the experimenter, so that the bird cannot find the cache simply by seeing or smelling the food itself. To determine how likely the bird would be to search a particular place had it not stored food there, a variety of control procedures are used. One method is to allow the bird to search the empty aviary for a period of time immediately before each episode of food storing. This control period provides an estimate of any bias or preference to search particular places whether food has been stored there or not. Comparison of actual cache recovery behavior to behavior during the control period can be used as a measure of whether the birds remember the locations of their caches (Sherry et al. 1981; Sherry 1982, 1984a). Another method is to compare, during cache recovery, the probability of a bird's visiting a site given that food has been stored there, to the probability of a bird's visiting that site given no food storage (Shettleworth and Krebs 1982, 1986). The arrangement of moss beds or trees in the aviary can be changed between one caching trial and the next in an attempt to present the birds with a novel arrangement of sites in which to cache.

Both Marsh Tits and Black-Capped Chickadees perform well under these conditions and return to their cache sites much more accurately than would be expected from control data. They also return to caches at a much higher rate than expected by chance, which can be calculated from the total number of searches and the proportion of sites in which food had previously been stored. Birds can relocate their cache sites accurately when there is no stored seed that they might see or smell (Sherry et al. 1981; Sherry 1982, 1984a). Indeed they are not very adept at finding seeds stored by other birds or seeds moved to different locations by the experimenter (Shettleworth and Krebs 1982, Baker et al. 1988). Neither Marsh Tits nor Black-capped Chickadees have been observed to cover caches or to mark cache sites in any way.

The birds do not need to choose cache sites according to a rule in order

to perform well during cache recovery. First, sites do not vary much under laboratory conditions, whether they are beds of moss or holes in tree branches. Second, when the experimental arrangement of cache sites is slightly different for each bout of caching, the use of particular sites conforms to a Poisson random distribution, indicating that re-use of particular sites occurs on a chance basis rather than a rule-governed basis. Under a different experimental procedure, cache site preferences do develop (Shettleworth and Krebs 1982). However, the birds are more likely to search a site after food has been stored in it than when food has not been stored there, whatever the level of preference for that particular site.

It might be supposed that the birds would use the order in which seeds were stored as a mnemonic device to assist in returning to cache sites, but correlations between storage sequence and recovery sequence are sometimes positive, sometimes negative, and usually non-significant (Sherry 1984a, b). Birds are more likely to visit more recently made caches if an interval of a few hours intervenes between one bout of storage and the next, but this is probably an effect of decay or interference in memory, rather than reliance on the sequence of caching as an aid to recall (Shettleworth and Krebs 1982).

Convincing evidence that memory is the major means of cache recovery comes from experiments in which the birds are allowed to retrieve successfully some stored seeds. If memory is used to relocate cache sites, then it makes little functional sense for the bird to remember all cache sites it has recently established, because some of these will be empty as a result of the bird's own retrieval behavior. Both Marsh Tits and Black-capped Chickadees handle this problem with little difficulty (Sherry 1982, 1984a). Birds were allowed to store about twelve seeds, and on the following day retrieve half of what they had stored. On the day after that, they were allowed to search for caches again, all remaining seed having been removed in the meantime by the experimenter. The birds returned to caches they had not previously harvested and did not search at caches they had. Neither the chance encounter nor the rule hypothesis can account for this result. Instead, sites which no longer contain food are distinguished in memory from sites where food remains, even though both kinds of sites were originally established during the same bout of caching. The same result occurs if birds simply discover that food has been removed from a cache (Sherry 1984a). That is, they do not have to retrieve the food themselves to be able to avoid subsequent visits to empty cache sites.

MEMORY AND THE HIPPOCAMPUS

A recent development in the study of memory in food-storing parids has been to look directly at structures in the brain with memory functions.

In mammals, the hippocampus plays an important role in memory. There are two dominant theories of the involvement of the hippocampus in memory, the cognitive mapping hypothesis (O'Keefe and Nadel 1978) and the working memory hypothesis (Olton et al. 1979). The cognitive mapping idea holds that the hippocampus processes spatial information and is essential to knowledge of places and relations among places. The evidence for this comes from the firing pattern of single cells in the hippocampus, some of which have receptive fields that are places. That is, a cell is active when the animal is in a particular place, for example a corner of its enclosure, and inactive when the animal leaves that place (O'Keefe and Dostrovsky 1971, Best and Ranck 1982). Surgical or neurochemical damage to the hippocampus can be shown to disrupt spatial orientation (Morris et al. 1982).

The working memory idea holds that memory can be dichotomized into two functions: reference memory, which retains information necessary to all performances of a particular task, and working memory, which only retains information about the current performance of the task (Honig 1978). For example, the rules of chess might be retained in reference memory, but how the board position of the present game developed is retained in working memory. The theory of Olton and his colleagues is that the hippocampus plays a role in working memory, regardless of whether the contents of memory are spatial. The evidence in support of this idea comes from studies of the behavior of rats on various tasks in which it can be shown that damage to the hippocampus disrupts memory for ongoing performance but not memory for the nature of the task (Walker and Olton 1984).

Because of the importance of the hippocampus in memory, we examined the effects of hippocampal aspiration on cache recovery by Black-capped Chickadees (Sherry and Vaccarino, 1989). The approach seemed promising because a study by Krushinskaya (1966) had shown that food-storing Eurasian Nutcrackers (*Nucifraga columbiana*) were unable to relocate their caches after lesions of the hyperstriatum, the part of the brain where the hippocampus is found in birds. Chickadees were allowed to cache and recover seeds once a day for five days. The hippocampus was aspirated bilaterally under anaesthetic, and the birds were allowed to recover from surgery. Three days later caching and recovery trials began again and continued for five days. We found that birds with hippocampal damage performed very poorly at cache recovery, compared to unoperated control birds and birds with aspirations of a comparable size in the hyperstriatum accessorium. They continued to cache seeds and search for them as intensely as other birds, but their cache recovery attempts were no more accurate than chance.

To determine whether this effect was due to disruption of cognitive mapping or working memory, or indeed whether it was due to a memory deficit at all, we conducted a further experiment. Chickadees were trained to locate seeds hidden by the experimenter in the same array of tree branches used for caching. In the Place task six seeds were hidden among the seventy-two holes available, but always in the same places. To perform successfully the bird had to remember which six places contained food. In the Cue task six seeds were hidden, but always in different places. Which six places held seeds was indicated by cues placed near each hole. The six holes with seeds had a small white card beside them, while all the other holes had small black cards. For half of the birds the colors of the cards indicating holes with seeds and empty holes were reversed.

Chickadees with hippocampal damage performed normally on the Cue task but were impaired on the Place task. Unoperated controls and birds with aspirations placed in the hyperstriatum accessorium performed both tasks normally. This is the result that the cognitive mapping account of hippocampal function would predict. To determine whether there was any detectable effect of hippocampal damage on working memory, we tallied all revisits to holes previously inspected. These revisits were regarded as working memory errors because the bird had already determined within that trial that the site had a seed in it (which it took) or was empty to begin with. Birds with hippocampal damage made far more revisits than control birds, a result predicted by the working memory account of hippocampal function.

These experiments showed that the avian hippocampus functions very much like the mammalian hippocampus with respect to memory. Experiments with homing pigeons have also shown that the avian hippocampus serves important memory functions, such as recognition of the home loft (Bingman et al. 1985). Although cognitive mapping and working memory are often presented as alternative accounts of hippocampal function, the results with chickadees, like other recent results with mammals (Jarrard et al. 1984), suggest that the hippocampus serves both functions. It is possible that the hippocampus has multiple memory functions (Sherry and Schacter 1987) or that cognitive mapping and working memory are two manifestations of the same underlying process. Because neurophysiological disruption of memory impaired cache recovery, the results also confirm that memory for cache sites is an essential component of cache recovery.

COMPARATIVE STUDIES OF THE HIPPOCAMPUS

Not all parids store food, and most avian families do not include food-storing species. Anthony Vaccarino and I compared the hippocampus of

storing and non-storing species, with interesting results. Prompted by studies of variation in the volume of song control nuclei of birds (Nottebohm et al. 1981), we compared the volume of the hippocampus in Black-capped Chickadees, Marsh Tits, Great Tits, and Blue Tits (the latter three kindly provided by John Krebs at the Edward Grey Institute, Oxford). Black-capped Chickadees and Marsh Tits store food, Great Tits do not, and the food-storing status of Blue Tits is uncertain. (There are several anecdotal reports of food storing by Blue Tits, but more extensive observations have failed to detect storing in this species; see Table 1.) We found that the hippocampus makes up about 5% of the telencephalon in the food-storing species, about 3% in the Great Tit, and is of intermediate size in the Blue Tit. Promising as this result is, without data on hippocampal size in more non-storing parids it is difficult to interpret. Hippocampal size in storing and non-storing families of birds is a better comparison, because it makes available a larger set of data to work with and permits a more rigorous treatment of allometric and phylogenetic effects (Harvey and Mace 1982). Comparisons of the size of the hippocampus among 13 families and subfamilies of North American passerines (Sherry et al. 1988) and nine families of European passerines (Krebs et al., in press) show that the three food-storing families, Paridae, Sittidae, and Corvidae, all have a larger hippocampus than expected for their body weight or for the size of their telencephalon. It is likely that reliance on stored food in these families has led to selection favoring memory capacities equal to the task of recovering stored food, and the effects of this selection can be seen in the size of the hippocampus, a structure intimately involved in memory for cache sites.

WHY DO PARIDS STORE FOOD AND OTHER QUESTIONS

Many questions remain unanswered about food storing in chickadees and tits. One of the clearest and perhaps the easiest to answer is, which species show this behavior and which do not? Food storing is not difficult to detect for an observer attuned to its possible occurrence, and the methods of Haftorn (1954), Moreno et al. (1981), and Cowie et al. (1981) can provide a great deal of descriptive detail about the behavior.

A more difficult problem, but the central one from an evolutionary point of view, is why do some parids store food while others do not? The one known non-storer *P. major* is larger than other European tits, which not only has energetic consequences, but also results in its being dominant to other tits at rich food sources such as artificial feeders. Large body size and dominance may remove some of the selective pressures that maintain food storing in other tits. The center of the Great Tit's distribution is farther south than those of other European tits (Perrins 1979), and this

may account for its being less adapted to seasonal fluctuations in food availability. The Great Tit's range also extends farther north, however (Haftorn 1957), so exposure to seasonal fluctuations in food availability cannot be the whole answer.

In addition to variation within the Paridae, there is also variation among families of birds in the occurrence of food storing. Diet, body size, and seasonality of the food supply may all be important determinants of whether or not food storing occurs. Memory equal to the task of recovering scattered caches seems an evolutionary prerequisite for food storing, although an evolutionary scenario in which rudimentary food storing occurred first, followed by adaptive change in memory seems equally likely. Richards (1958) has raised the interesting possibility that some methods of feeding may lend themselves to leaving pieces of food behind to be collected later. Nuthatches, for example, wedge food into bark crevices to assist in handling it. The feeding methods of certain groups may provide the raw material for the evolution of more complex storing behavior.

A question alluded to earlier is: "how long after food stores are created are they harvested?" The interval appears to be only a few days for Marsh Tits, but there are indications of more long-term use of food stores in other species. This may vary between species, or it may be determined by local ecological conditions.

It is clear why storing food for long periods could increase fitness. There may be no food available in winter except that which was cached the previous autumn, and a supply of stored food could permit earlier breeding or feeding of the young than would be possible without such a reserve. It is less obvious what the fitness gains are from storing food for a period of a few days. Nonetheless, a number of benefits from short-term storing can be proposed. By storing food, small birds like chickadees and tits may be able to obtain a larger proportion of a rich food source than they would if they simply ate until other animals displaced them or depleted the source. Alternatively, there may be fluctuations in food availability on the scale of a few days, or even within days, that would be mitigated by a reserve of stored food. The effects of short-term fluctuations in energy requirements could also be reduced if stored food were available. Lack (1954) proposed that stored food allows rapid feeding in the morning following the overnight fast, though in fact the reverse appears to be true. Marsh Tits and some other food-storing birds do most of their cache recovery at the end of the day (Collopy 1977, Powlesland 1980, Rijnsdorp et al. 1981, Stevens and Krebs 1986). Caches are probably used as a reliable source of food to be eaten just before beginning the overnight fast. McNamara and Houston (1986) analyzed how food eaten at various times during the day contributes to overnight survival of small birds in

winter, and they found that food eaten just before nightfall can make a much larger contribution to survival than the same food item eaten earlier in the day. Short-term food storing may effectively raise the value of food items by deferring their consumption until the time when they make the greatest contribution to fitness.

In scatter hoarding species, the spacing among neighboring caches has a major effect on the loss of stored food to other animals. This density dependence occurs because animals finding one cache by chance search the surrounding area for more (Stapanian and Smith 1978, 1984; Clarkson et al. 1986). If neighboring caches are placed outside this zone of area-restricted search, then an animal finding one cache by chance cannot systematically pilfer others. Spacing caches is a way of safeguarding them (Vander Wall and Smith, 1987). Marsh Tits maintain a spacing among their caches that minimizes the loss of stored food to other animals (Sherry et al. 1982), but how they space their caches as they do is not well understood. Similarly, how far food is carried from the point where it was first encountered appears to be influenced by a variety of little-understood factors (Clarkson et al. 1986).

A bird makes a decision each time a food item is stored. This "decision" need have no element of reason or foresight (despite Perna's intuitions quoted at the beginning of the article), no more so than reason or foresight are used, for example, by migratory birds to control their annual movements. But decisions about whether to eat a food item or store it, whether to place it a meter away or a hundred meters away, whether to hide it on the ground or high in a tree, whether to retrieve it promptly or to leave it in place, are going on continually. Behavioural ecologists have enjoyed some success in modelling such economic decisions (Stephens and Krebs 1986). A great deal more information is necessary before the consequences of various food-storing decisions can be analyzed, but a start has been made and this may prove to be a fruitful line of inquiry.

Finally, the food-storing habit may have far-reaching social consequences (Roberts 1979). Reliance on stored food has major effects on social organization in Acorn Woodpeckers (*Melanerpes formicivorus*) (Stacey and Bock 1978), and Ekman (1979 and this symposium) has suggested that dispersal patterns, site tenacity, and other features of Parid social organization may be adaptations to food storing.

Despite much recent progress, many questions about the ecology, behavior, and evolution of food storing remain unanswered. The Paridae are a group well-suited for examination of these problems, and as the members of this family of birds become better known, some answers may be forthcoming.

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